Biology of the Spider *Diguetia imperiosa*[1]

(Araneida: Diguetidae)

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Spiders of the family Diguetidae have a unique type of web and cocoon construction. They spin a sheet web surrounded by a tangled mesh of silk threads, and build a retreat which serves as protection for the spider, and in the case of females, as an enclosure for the egg sacs. Diguetids are considered to be relatively primitive spiders and the genitalia of both sexes are comparatively simple. The family was established by Gertsch (1949) and also revised by Gertsch (1958). The nine species of the family all belong to the genus *Diguetia* and are distributed from the southwestern United States through Mexico, and also occur in western Argentina. Although the diguetids are often locally abundant, few studies of their biology have been made. Cazier and Mortenson (1962) studied the biology of *Diguetia canities* near Portal, Arizona; Gerschman de Pikelin and Schiapelli (1962) described the web structure of *D. catamarquensis* in Argentina, and Eberhard (1967) studied attack and prey-wrapping behavior in *D. albolineata.*

In August 1968 I had the opportunity to make field studies of *D. imperiosa* Gertsch and Mulaik (Fig. 1), a species distributed widely through the southwestern United States and northern Mexico. Field work done in the Cuatro Ciénegas Basin of Coahuila, Mexico. Spiders and retreats were brought to California for observations on behavior and reproductive biology.

METHODS AND MATERIALS

To study habitat, web structure, and behavior of *Diguetia imperiosa* in the field, twenty webs were located, marked, and observed from 9 to 14 August 1968.

To determine fecundity and details of retreat construction, 45 retreats and the spiders accompanying them were collected on 14 August and were fixed and preserved using the methods recommended by Williams (1968). Egg counts and dissection of retreats were done using a binocular dissecting microscope, and measurements were taken with an

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ocular micrometer. Maturity of female spiders was determined by examination of the ovaries.

Ninety retreats with the accompanying spiders were collected on 15 August 1968 and were reared in the laboratory until 31 December 1969. Ten female spiders were allowed to construct webs in small bushes simulating vegetation in the natural habitat; the remainder were confined in small plastic boxes. Laboratory temperatures varied from 20° to 30° C and an approximate 12 hour photoperiod was maintained. Food (*Tenebrio molitor* larvae and adult *Drosophila* sp.) and water were offered at weekly intervals.

Stridulation was recorded with a Sennheiser microphone and a Nagra IIIB tape recorder (15 inches per second). A sound spectrogram was prepared using a model 661-B Sona-Graph manufactured by the Kay Electric Company.

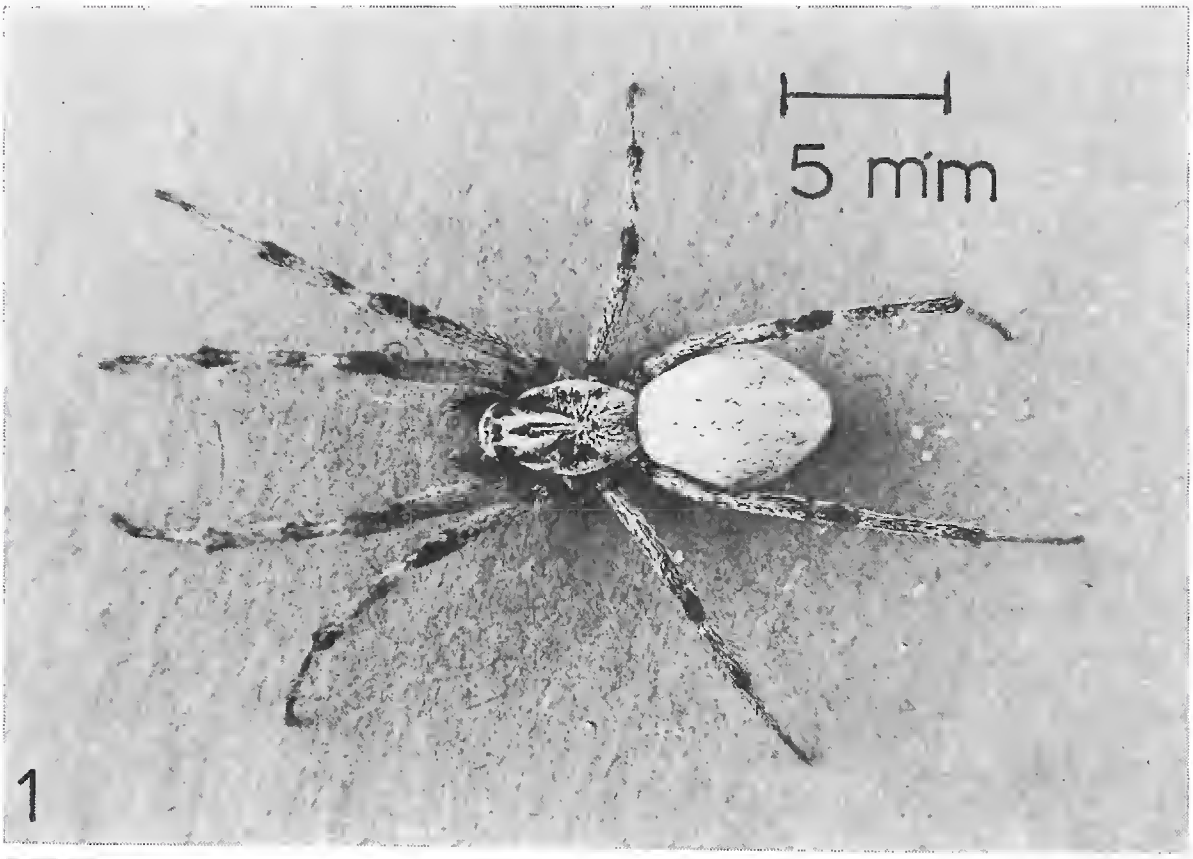
Results

Study area.—Field work was carried out seven kilometers southwest of the town of Cuatro Ciénegas de Carranza, Coahuila, Mexico. Cuatro Ciénegas lies in an intermontane basin on the east edge of the Mesa del Norte. The basin measures about 30 by 40 km. An arid Chihuahuan climate prevails, but large numbers of springs give rise to complex systems of internal drainage within the basin. Minckley (1969) has summarized biological research in the Cuatro Ciénegas area.

The study area consisted of low dunes and flats. The dunes were stabilized and of high gypsum content. The flats had powdery soil and were only slightly elevated above the water table; it appeared that flooding was of seasonal occurrence. Zonation of the soil was lacking, and vegetation was sparse. Flats were primarily vegetated by chenopods (*Allenrolfea occidentalis* (Wats.) Kuntze, *Suaeda* spp.) and unidentified sedges. Dunes supported yucca (*Yucca* sp.), mesquite (*Prosopis glandulosa* Torr.), ocotillo (*Fouquiera* sp.), and two species of *Opuntia.*

Web and retreat structure.—*Diguetia imperiosa* constructed its web in spaces between the branches of low plants, or suspended it between adjacent plants. All webs observed were less than one meter above the ground. Orientation of the web appeared to be non-random; 75 per cent of the webs observed were suspended on the west facing side of the supporting plants.

The web invariably was composed of four structural parts (Fig. 2). Hereafter, the term "web" will refer to the entire web, and the term "webbing" will refer to the various parts of the web. The parts of the



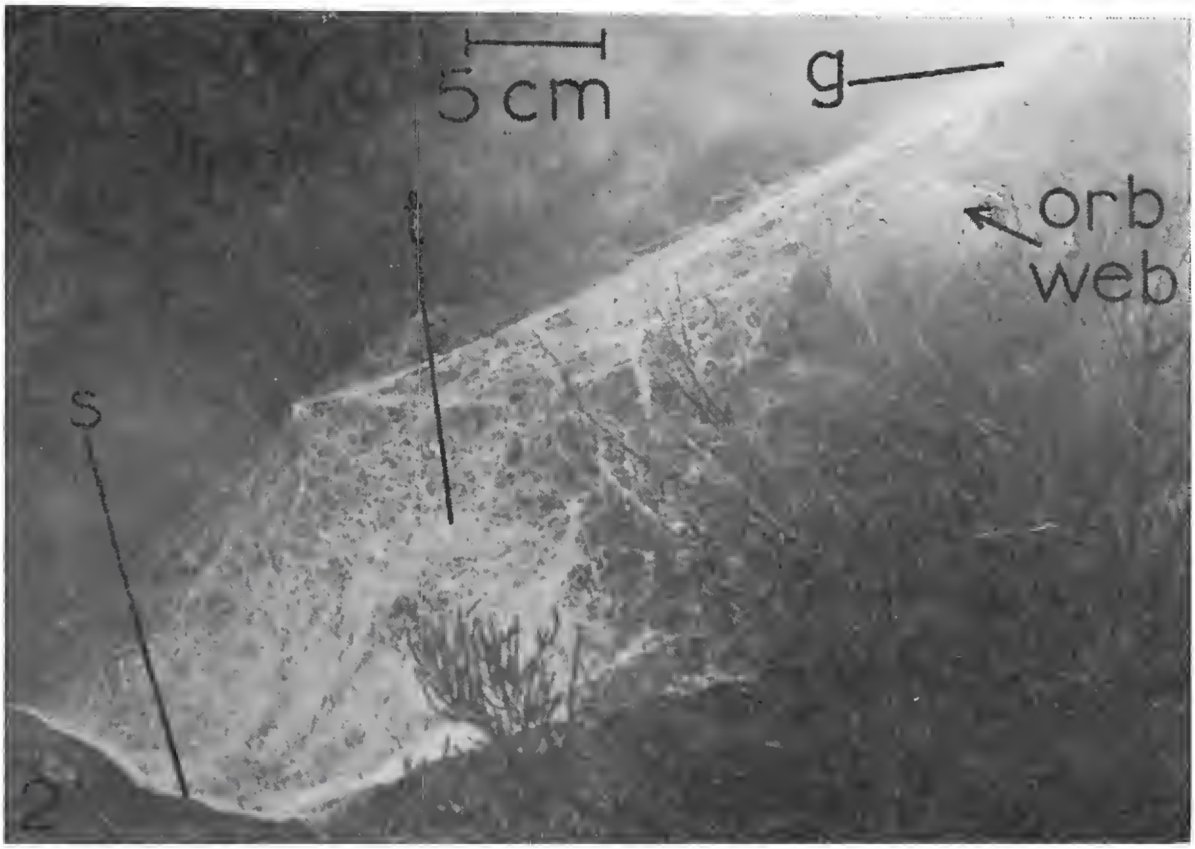
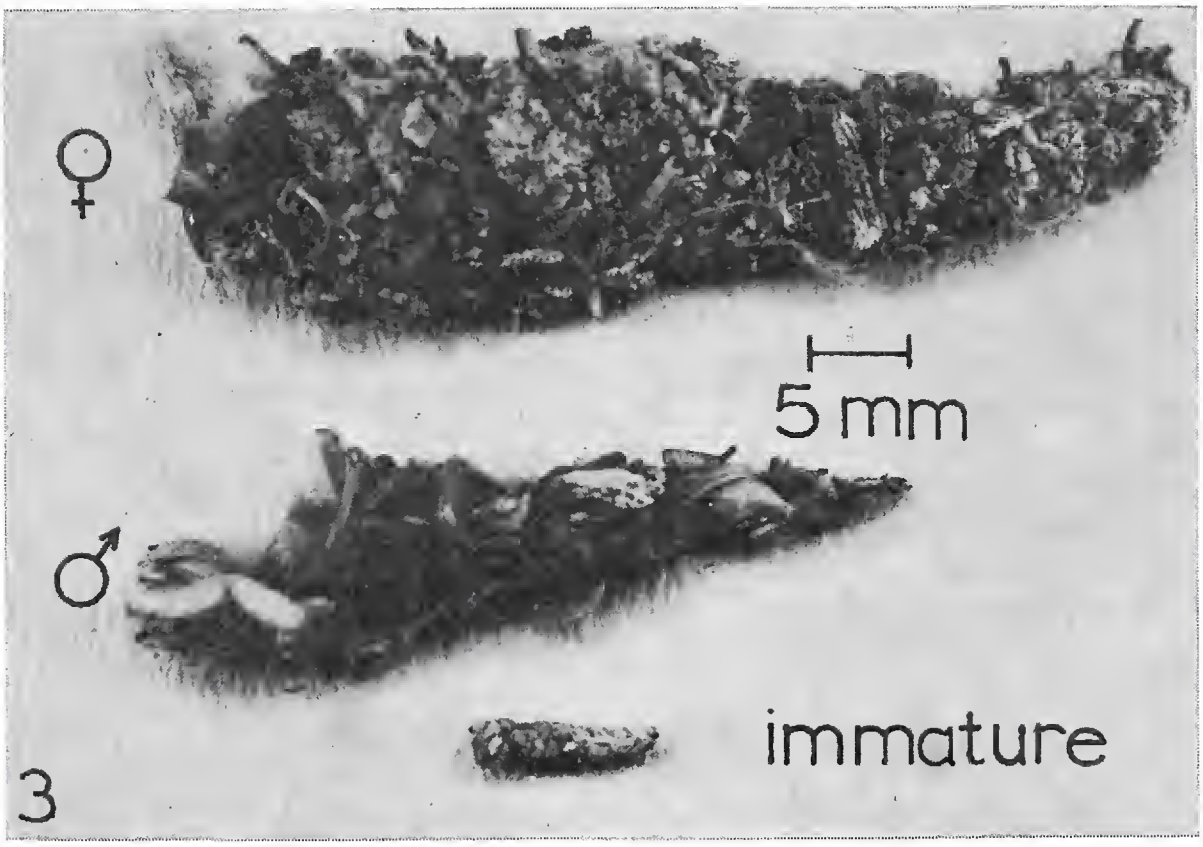


FIG. 1. Adult female *Diguetia imperiosa* Gertsch and Mulaik from Cuatro Ciénegas de Carranza, Coahuila, Mexico. Photo by Carolyn Cavalier. FIG. 2. Web of female *Diguetia imperiosa* near Cuatro Ciénegas de Carranza, Coahuila, Mexico. Guy lines (g), tangle webbing, and sheet webbing (s) are visible. Orb web of *Metepeira* sp. is located in upper right portion of *D. imperiosa* web.

Table 1. Accessory materials used by *Diguetia imperiosa* in retreats construction. Analysis based on dissection of 30 retreats collected 15 August 1968 near Cuatro Ciénegas de Carranza, Coahuila, Mexico.

Material	No. of retreats	% occurrence
Plant Material		
Leguminosae: *Prosopis glandulosa Torr.*	24	80
Cactaceae: *Opuntia* spp.	3	10
Cyperaceae: unidentified sedge	4	13
Chenopodiaceae: *Suaeda* spp. and *Allenrolfea occidentalis* (Wats.) Kuntze	7	23
Arthropod Material		
Arachnida: *Diguetia imperiosa* exuvia	8	26
Salticidae	1	3
Araneidae	1	3
Insecta: Coleoptera: Oedemeridae: *Oxacis* sp.	14	47
Scarabeidae	9	30
Bostrichidae, Coccinellidae, Curculionidae, Tenebrionidae	4	13
Hymenoptera: Myrmicidae: Myrmicinae	14	47
Orthoptera: Acrididae	4	13
Lepidoptera: unidentified moths	4	13
Diptera: Muscidae	1	3
Hemiptera: Coreidae, Corixidae, Pentatomidae	3	10
Homoptera: Cicadellidae	4	13
Cercopidae, Psyllidae, Cicadidae	3	10

web were the guy lines, the tangle webbing, the sheet webbing, and the retreat. The guy lines extended to the apices of the branches of the supporting plant and provided suspension for the web. They consisted of multiple strands of heavy silk. The tangle webbing consisted of an irregular mesh of silk which filled the area above and below the sheet webbing. The sheet webbing consisted of a fine silk mesh radiating horizontally from the centrally positioned cocoon; it was oval to roughly circular in shape and was no greater than 0.3 m^2 in area. Neither tangle nor sheet webbing consisted of viscid silk. Each spider had one retreat associated with its web. The retreat was of a characteristic conical shape, and was open at the lower end. It was suspended by strong strands of silk which were connected to the guy lines and to plant branches, and always hung vertically in the web. The internal diameter of the retreat was sufficiently large to allow the spider to completely



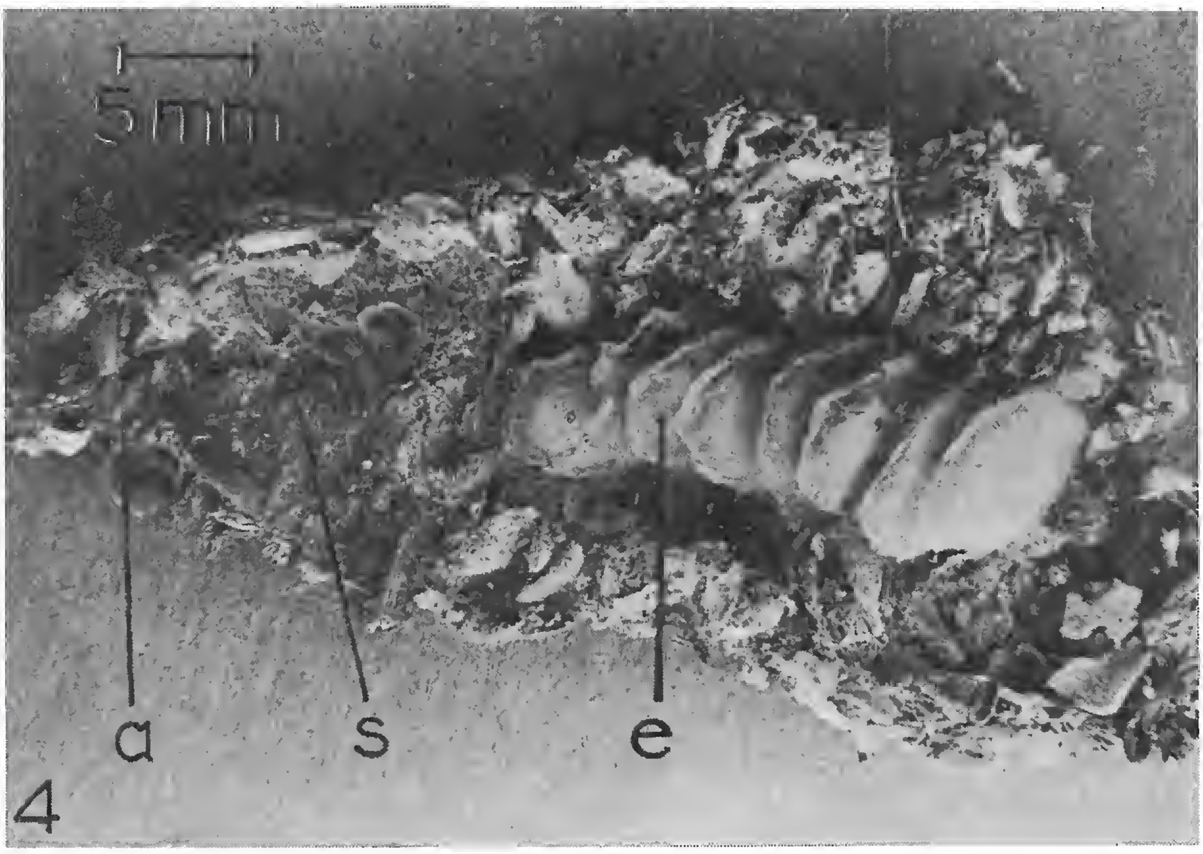


FIG. 3. Retreats of female, male, and immature *Diguetia imperiosa*. FIG. 4. Retreat of female *Diguetia imperiosa*. Opened retreat shows egg sacs with silk cover removed. a = accessory materials, s = silk mesh, e = egg case.

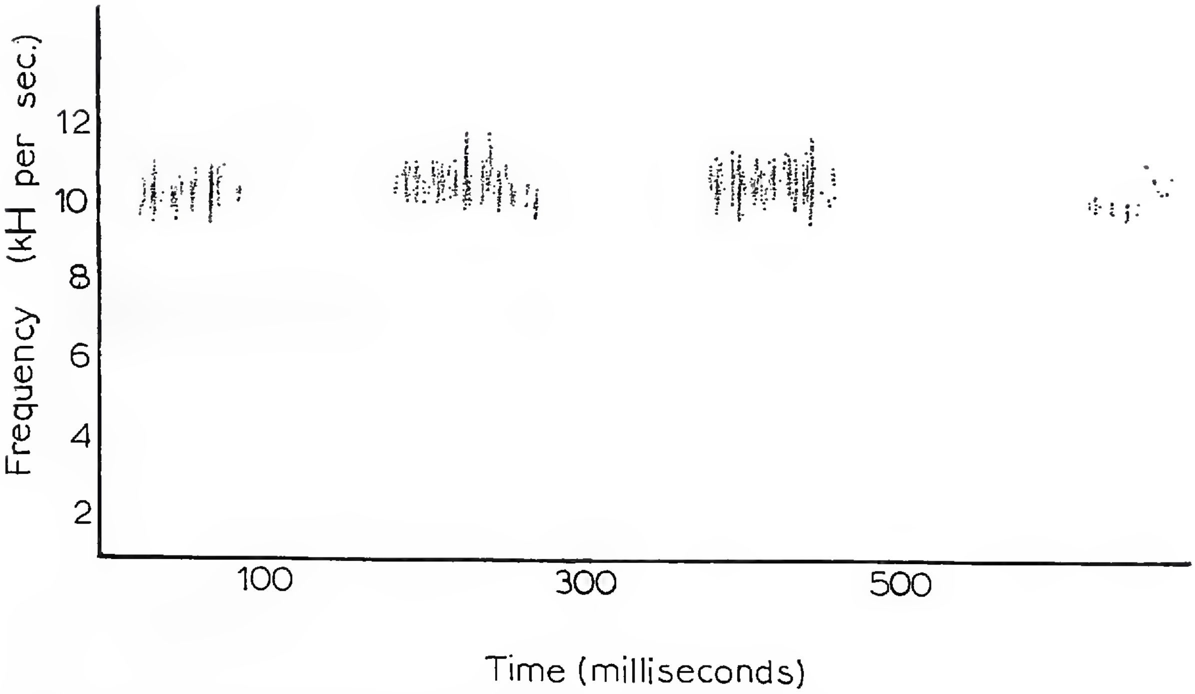


Fig. 5. Sound spectrogram of stridulation of adult female *Diguetia imperiosa*, recorded in laboratory 15 December 1968.

enter; access was from the underside of the sheet webbing. The retreat was constructed of accessory materials, such as plant leaves, insect bodies, and other objects, tightly bound together with a fine silk mesh (Fig. 3). Mature females laid a series of egg sacs inside the retreat in an overlapping, shingle-like arrangement (Fig. 4). The first egg sac laid was placed near the upper, closed end of the retreat. The egg sacs were disc-shaped and about 8 mm in diameter. They were formed by two densely woven discs of silk weakly joined at their peripheries. Each egg sac was covered with a coarse silk mesh with the strands spaced widely enough to allow free passage of emerging spiderlings.

Retreats of mature females were larger and of more tightly woven construction than the retreats of males. Retreats of immature spiders were constructed of materials of smaller, more uniform size than the retreats of mature spiders (Fig. 3).

To determine what accessory materials were used in retreat construction, 30 retreats were dissected. Leaves and twigs of mesquite (*Prosopis glandulosa* Torr.) and Chenopodiaceae were the commonest plant materials, and oedemerid beetles (*Oxacis* sp.) and ants were the commonest insects (Table 1).

Behavior of spiders in the web.—*Diguetia imperiosa* was primarily nocturnal, remaining inside the retreat during the day. However, spiders left the retreat at any hour, day or night, to capture prey. They also left the retreat during the period of midday high temperature, which

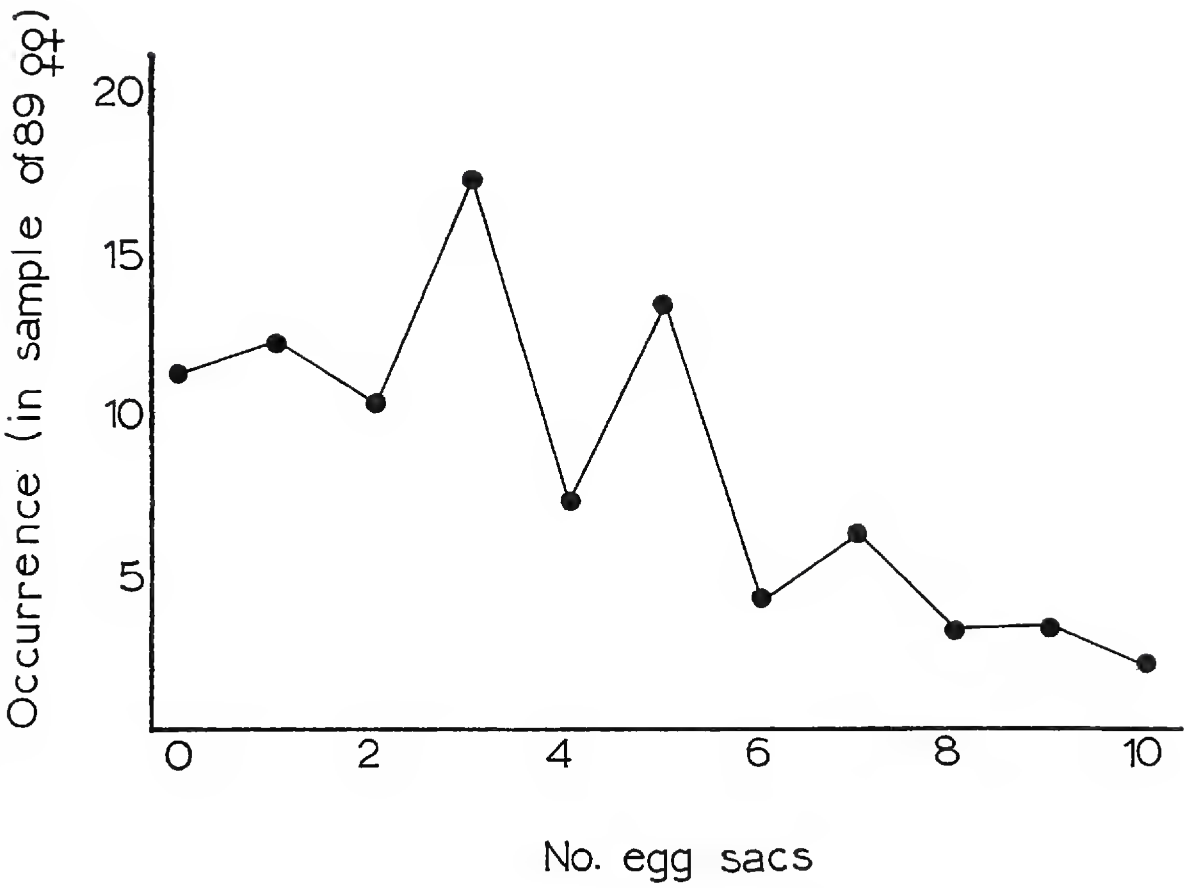


Fig. 6. Occurrence of egg sacs in 89 retreats of female *Diguetia imperiosa.*

reached as much as 47° C during the field study. At this time the spiders positioned themselves in the web so that they were in the shadow cast by the retreat. Later in the afternoon the spiders always returned to their retreat. It was not determined if spiders would leave the retreat at midday on cool or overcast days. At dusk, spiders again left the retreat and remained exposed on the underside of the sheet webbing during the hours of darkness. To study web-building techniques of *D. imperiosa* in the field, the webs of two adult females were removed on 12 August. The spiders and their retreats were left in the supporting plants. The spiders replaced the guy lines supporting the retreat first, then erected guy lines to support the sheet and tangle webbing. Spinning of sheet and tangle webbing followed; but three days later, when field observations ceased, only sparse webs had been constructed. The incomplete nature of the sheet and tangle webbing suggested that prey capture would have been severely reduced.

In the laboratory, spiders began to construct webs in the same manner as individuals in the field, but after a month they still had not constructed complete webs.

Diguetia imperiosa reacted to web disturbance in three different ways. Slight movements in any part of the web induced attack behavior.

Disturbances of a greater magnitude, involving significant movement of the entire web, caused spiders to withdraw into the retreat. This response occurred when capture of spiders was attempted in the field. Sudden severe disturbance to the whole web, or destruction of the web, caused spiders to drop from the web and remain motionless on the ground in a death feigning posture, in which the legs were drawn close to the body, and no movement occurred for as long as 45 minutes. Spiders later returned to the web area by climbing the nearest plant. No drag lines were established in these abrupt falls from the web.

Two webs in the study area each contained a male-female pair of spiders. In both of these webs the female had already deposited eggs, and no mating activity was observed. When prey entered the webs of these paired spiders, females attacked and handled the prey in the usual manner, but males did not respond. When disturbed, in each case the females withdrew into the retreat in the same way as single females, but the males ran about the web. In one instance a male did attempt to enter the female's retreat after she had withdrawn, but he emerged almost immediately.

Prey became trapped either in the tangle webbing or on the sheet webbing. When prey entered the web, the spider ran out on the underside of the sheet webbing toward the source of disturbance. In a few instances, spiders shook the sheet webbing when approaching prey. If prey remained trapped in the tangle webbing, spiders had to climb into the tangle webbing to attack. In this situation, a spider would run to the edge of the sheet webbing to ascend the tangle webbing; no use of holes in the sheet webbing to pass from one side to the other was observed. In most of the prey captures observed in the field, the spiders encountered and attacked prey on the sheet webbing. Spiders attacked from the underside of the sheet webbing in these cases. The first pair of legs were extended through the sheet webbing to hold the prey down while it was bitten through the sheet webbing; the hold on the prey was then released. When the prey ceased struggling, the spider cut a hole in the sheet webbing with the chelicerae, and pulled the prey through to the underside of the sheet webbing.

When prey capture occurred at night, feeding took place in an exposed position out under the sheet webbing, but prey captured during the day was carried to a location just beneath the retreat to be eaten.

When spiders captured large winged insects, a simple form of prey wrapping occurred. The prey was suspended from a silk line and rotated while a few turns of silk were used to bind the wings. Small prey was

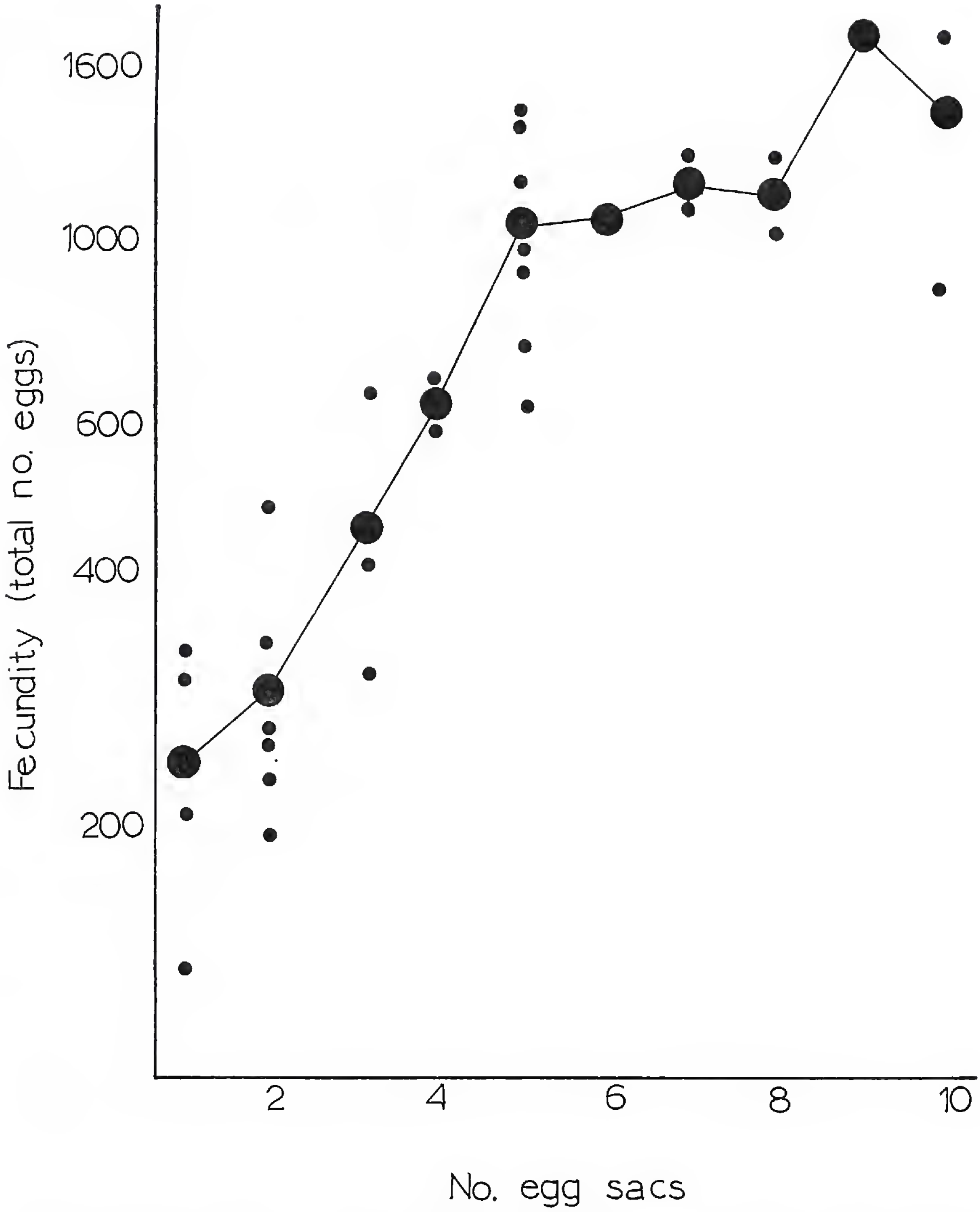


Fig. 7. Egg production of 30 female *Diguetia imperiosa*. Small dots represent totals of individual retreats; large dots represent mean totals.

captured and eaten without the use of silk. Prey wrapping was also observed when an insect became trapped in the web while the spider was feeding on previously captured prey. The first prey was suspended and wrapped; then the spider attacked the new prey.

When a nonprey item such as a piece of plant material fell onto the sheet webbing, spiders discarded the item after a few seconds of exploratory contact using the pedipalps and first pair of legs; a hole was cut in the sheet webbing with the chelicerae and the object was permitted to drop to the ground.

Attack behavior of captive *D. imperiosa* did not differ from that observed in the field.

Stridulation.—Stridulation was observed in several adult female *D. imperiosa* in the laboratory when the spiders were physically disturbed, as when grasped by forceps. The stridulatory mechanism in the genus *Diguetia* consists of fine grooves on the outer face of the paturon of the chelicerae, which serve as a file, and a row of small tubercles on the prolateral side of the femur of the pedipalp, which serve as a scraper. During stridulation, the chelicerae are spread and the pedipalps are simultaneously rapidly raised and lowered. In *D. imperiosa*, the resultant sound occurred in bursts lasting for 75 milliseconds, separated by 100 millisecond intervals. The frequency averaged about 10,000 Hertz (Fig. 5). Males had fewer and smaller femoral tubercles than females, but no live males were available for recording stridulation.

Associates.—Two species of spiders were directly associated with *Diguetia imperiosa* webs in the field. Immature spiders of an undetermined species of the araneid genus *Metepeira* were found as a commensal in 25 per cent of the *D. imperiosa* webs examined in the field. *Metepeira* constructed a small orb web in the upper tangle webbing of the host spider. These orb webs were less than five centimeters in diameter and were vertically oriented. No mature *Metepeira* were found associated with *D. imperiosa*.

Two webs examined in the field each contained an individual of an undetermined species of the genus *Mimetus*, spiders predaceous on web building spiders. In both cases the *D. imperiosa* which had constructed the web was missing.

No parasitization or predation of egg sacs was found.

Reproductive biology.—Descriptive terms of development are those used by Hite *et al.* (1966). Eggs of *D. imperiosa* were white, spherical, and varied from 0.45 to 0.55 mm in diameter. When eggs hatched a first stage postembryo emerged. This first stage postembryo was covered with a thin membrane through which the developing spider could be seen. The first stage postembryo was yellowish white except for black eyes, and ranged from 0.53 to 0.62 mm in length. The second stage postembryo was free moving and possessed tarsal claws, but lacked development of cheliceral fangs and body pigment. This stage ranged from 0.80 to 0.90 mm in length. The next molt gave rise to spiderlings with fully developed claws, chelicerae, and body pigmentation resembling that of the adult. The range in body size was the same as the

TABLE 2. Egg production by *Diguetia imperiosa*. Based on egg sacs contained in seven retreats, each with five egg sacs, collected 14 August 1968. Number of eggs and young in each sac is represented.

	Individual						
Egg sac (oldest to newest)	#102	#103	#104	#130	#134	#135	#137
(first egg sac laid)	70	236	181	262	321	415	190
	200	217	261	206	269	367	148
	178	162	253	208	222	268	110
	167	152	200	125	244	241	151
(last egg sac laid)	206	128	246	140	289	75	107
mean	164	179	228	188	269	273	141

F-Test Analysis

Source of variation	DF	Sum Squares	Mean Square	F	P
total	34	197622			
retreat	6	79848	13308	3.56	$P < 0.01$
position of egg sacs	4	28040	7010	1.87	$P < 0.05$
error	24	89734	3738		

second stage postembryo. Development to the spiderling stage occurred within the egg sac. The first and second stage embryos were inactive, developmental stages, while the spiderlings were capable of feeding and silk production. Spiderlings escaped from the cocoon by splitting the egg sac along the loosely joined peripheral seam. The emergence of spiderlings from the retreats took place in the laboratory from 22 August to 23 September 1968. At this time emergence had occurred in only 43 per cent of the 56 retreats containing eggs. No emergence occurred after 23 September. Nonemerged spiderlings remained alive inside the egg sacs until December 1968. After this time all had died. Twenty-six per cent of the living females continued laying eggs until 23 September, 1968, whereas complete emergence from all egg sacs had already occurred in four per cent of retreats containing eggs collected on 14 and 15 August. Eggs laid in the laboratory failed to develop beyond the first stage postembryo.

Maturity of female spiders collected was determined either by the presence of eggs in the accompanying retreat or by examining the ovaries. In a sample of 30 mature females, the number of eggs laid per female ranged from none to 1,675, and the mean was 734. The egg sacs of 89 female retreats were counted. The number of egg sacs constructed per female ranged from zero to ten, with a mean of 3.6. Only 20 per cent of the females laid more than five egg sacs (Fig. 6).

Considerable variability existed in the numbers of eggs laid in subsequent egg sacs by the same spider. Some females laid progressively fewer eggs in later egg sacs, but others laid increasing numbers. Spiders which laid the same number of egg sacs during the reproductive season showed much variability in the egg number of corresponding egg sacs in the sequence, as well as in total number of eggs laid. This was shown by seven spiders which laid five egg sacs each (Table 2). Differences in the total number of eggs laid was highly significant ($F = 3.56$; $P < 0.01$). Based on the relative position within retreats, number of eggs laid in the corresponding egg sacs by the seven spiders, there was no pattern of increase or decrease in egg laying by these spiders ($F = 1.87$; $P > 0.5$). Similar results were found in a group of three spiders which laid three egg sacs each; there was a significant difference in total egg number laid by individual spiders ($F = 10.7$; $0.05 > P > 0.01$), and the group showed no pattern of differential egg laying in relation to the sequence of egg sacs ($F = 0.414$; $P > 0.05$).

No correlation was found between size of female spiders (carapace length) and total egg production, nor was there any indication of decreasing fertility in the later egg sacs.

Egg counts carried out on a sample of 30 retreats containing eggs showed that spiders laying over five egg sacs did not greatly increase their egg production over those which had laid only five egg sacs (Fig. 7). But egg production decreased sharply in spiders laying fewer than five egg sacs.

Of the 135 retreats collected, 89 had been built by females, 37 by males, and five by immature spiders. Of the 82 *Diguetia imperiosa* found with these retreats, 73 were mature females, four were mature males, and five were immature.

Discussion

Since nearly all the *Diguetia imperiosa* collected were mature, the spider probably has an annual life cycle, with one brood per year. A few females captured at maturity lived up to two additional years in the laboratory, but they did not molt, and became very inactive.

Stridulatory mechanisms of several types are widespread in spiders. In certain of the Theraphosamorphae stridulation occurs when the spider assumes a defensive posture, and the sound is readily audible to humans (Savory, 1928). Many araneomorph spiders have stridulatory organs, but the nature of the sound produced is generally unknown. The stridulation of *Diguetia imperiosa* is faintly audible to some human observers. As the stridulatory organ is found in both sexes, and since stridulation can be elicited by disturbing the females, a defensive function is indicated.

The lack of egg parasitization was surprising, since a fairly large sample of retreats and egg cases was examined for parasites. Cazier and Mortenson (1962) found both hymenopteran and coleopteran egg parasites of *Diguetia canities*, and five out of 75 retreats of *Diguetia* sp. from Yavapai County, Arizona sent to me by Dr. Cazier contained hymenopteran parasites. Suitable parasites may be absent in the Cuatro Ciénegas Basin, or parasites may have been operating at a low level when this study was done.

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LITERATURE CITED

CAZIER, M. A. AND M. A. MORTENSON. 1962. Analysis of the habitat, web design, cocoon and egg sacs of the tube weaving spider *Diguetia canities* (McCook). (Aranea, Diguetidae). Bull. S. Calif. Acad. Sci., 61: 65–88.

EBERHARD, W. 1967. Attack behavior of diguetid spiders and the origin of prey wrapping in spiders. Psyche, 74: 173–181.

GERSCHMAN DE PIKELIN, B. S. AND R. D. E. SCHIAPELLI. 1962. La familia Diguetidae en la Argentina. Physis, 23: 205–208.

GERTSCH, W. J. 1949. American spiders. D. van Nostrand Co., N. Y., 285 p.

1958. The spider family Diguetidae. Amer. Mus. Novitates, 1904: 1–24.

HITE, J. M., W. J. GLADNEY, J. L. LANCASTER, JR., AND W. H. WHITCOMB. 1966.

Biology of the brown recluse spider. Arkansas Agr. Exp. Sta. Bull. 711, 26 p.

Minckley, W. L. 1969. Environments of the Bolson of Cuatro Cienegas, Coahuila, Mexico. Texas West. Press Sci. Ser. 2, 65 p.

Savory, T. H. 1928. The biology of spiders. MacMillan Co., N. Y., 376 p.

Williams, S. C. 1968. Scorpion preservation for taxonomic and morphological studies. Wasmann J. Biol., 26: 133–136.

BOOK REVIEW

Ecological Studies 2. Integrated Experimental Ecology. Methods and Results of Ecosystem Research in the German Solling Project. Edited by Heinz Ellenberg. Springer-Verlag, New York, Inc. 214 p., 53 figs., 44 tables. 1971. $16.80.

One of the first International Biological Program (IBP) ecosystem studies was initiated in 1967 by the West German IBP Working Group for the Study of Terrestrial Biological Communities. A group of 50 scientists under the direction of Professor Ellenberg undertook an interdisciplinary study in the High Solling in the center of the Federal Republic of Germany. The area contains both forest and grassland ecosystems. This volume presents preliminary reports from many of the cooperative studies with emphasis on the methods used. A final report is expected after the conclusion of the project in 1972.

This volume contains 28 reports produced by 33 scientists. The introductory chapter by H. Ellenberg sets the background for the project by describing its relationship to IBP, the structure and functioning of ecosystems, the organization of the integrated research, and the research area and experimental plots. The remaining reports are subdivided into four major parts: Primary Production; Secondary Production; Environmental Conditions; and Range of Validity of the Results.

Insects are dealt with in four reports in Part 2: Secondary Production. These all involve food and energy turnover of various insects. Sampling techniques for studies of five species of leaf feeding weevils are described by W. Funke, with emphasis on the use of photo-eclectors (emergence traps). The report by K. Winter presents the approaches used to study some of 40 species of Lepidoptera, most of which are phytophagous on beech trees. Methods used to study energy flow in phytophagous and predatory arthropods are the subject of the report by W. Funke and G. Weidemann. The latter author also reports on the methods used to study population dynamics, standing crop, and production in predatory arthropods of the soil surface.

The basic thrust of the project is to develop a clear understanding of the biological basis of productivity using an integrated approach involving scientists from many disciplines. This volume presents only preliminary results and leaves one anxiously awaiting the production, assimilation and integration of the final reports. The main contribution of the present volume is the description of methodology which provides a valuable background for all ecologists.—Robbin W. Thorp, *University of California, Davis, 95616.*